STRESS AND ECOSYSTEMS

ARIEL E. LUGO*
Department of Botany and Center for Wetlands, University of Florida, Gainesville, Florida

ABSTRACT

The literature dealing with issues of stress as it affects ecosystems is reviewed. Definitions of stress are discussed. Models and literature examples are presented to illustrate the push—pull (positive—negative) effects of most stressors and to suggest that the point of attack and the type of stressor determine the rate of response of the ecosystem. Stressors with high-quality energies (highly concentrated energy sources) that divert low-quality energy flows in a system appear to have a greater impact than stressors with low-quality energy (diluted energy sources) that impact high-quality energy flows. It is suggested that ecosystem complexity (including species diversity, physiognomy, three dimensional organization, etc.) is a function of the balance between energies that contribute to growth and organization and those that contribute to disorder. The classification of environments by their "energy signatures" (the sum of all incoming energy flows into a system and the pattern of their delivery expressed on equal energy-quality basis) is presented as the best way to arrange and analyze ecosystems hierarchically according to their capacity to develop complexity and to tolerate stress. The patterns of ecosystem response to stressors, including positive, steady-state, and declining responses and possible extinction, are discussed. It is argued that, to solve the problems of ecosystem management and the issues of environmental impact, studies and analyses must be done at the level of the ecosystem and care should be taken to quantify both the stressor and the stress with units of comparable energy quality.

Today most of the biosphere has been altered in some way by the activities of man. With human impact on ecosystems becoming more obvious and more damaging to the economy of nations, the ecologist's interests are changing from descriptions of steady-state ecosystems to studies of ecosystem perturbations and their implica-

*Current address: Council on Environmental Quality, Washington, D. C.

tions to ecosystem structure, function, and stability. Sectors of the biosphere that are relatively more sensitive to human alteration (e.g., atmospheric and aquatic systems) initially received the greatest public attention. Terrestrial systems have been studied in relation to the impacts of ionizing radiation and radionuclide contamination (Woodwell, 1970). Marine and coastal systems are now under intense study as human population centers continue to grow in coastal areas and the demands for fossil fuel increase the intensity and frequency of oil and thermal pollution incidents (Cowell, 1971; Gibbons and Sharitz, 1974; Ferguson-Wood and Johannes, 1975). Another line of research uses laboratory microcosms to study the impact of heat, radiation, oil, and other pollutants on microecosystems (Byers, 1962; Moore, 1964; Copeland, 1965; Ferens and Byers, 1972; H. T. Odum, 1974).

Platt (1965), H. T. Odum (1967), Woodwell (1970), and others suggested that ecosystem response to external impact follows certain common patterns regardless of ecosystem type or type of impact. If they are correct, it would be unwarranted to continue to duplicate certain types of studies every time a new perturbation to the biosphere is introduced by man. If there are patterns of ecosystem response to stressors, we should use this knowledge to anticipate human impact on natural ecosystems. This paper has two objectives, first, to review the information available on the response of ecosystems to stressors to determine whether there are recurrent patterns of response, and, second, to suggest some approaches for the study of stress and natural ecosystems. The synthesis highlights controversial ideas with the hope of stimulating further research on the issue.

DEFINING STRESS AND STRESSORS

The concept of stress is commonly applied to describe the behavior of systems of all kinds. Meier (1972) summarized a number of definitions of stress: Stress was initially defined as "the forces or pressures exerted upon a material." Later, biological stress was defined as "the rate of all the wear and tear caused by life." In social studies, stress characterizes "physical, social, and cultural conditions likely to be discomforting for most people living within a specific group." Stress is also viewed as "a response to external or internal processes which reach those threshold levels that strain psychological and physiological integrative capacities close to or beyond their limits." Finally, stress can be defined as "any force that pushes the functioning of a critical subsystem beyond its ability to restore

homeostasis through ordinary, nonemergency adjustment processes."

Selye (1956) and Fitch and Johnson (1977) distinguished between stress and stressors. A stressor is any condition or situation that causes a system to mobilize its resources and increase its energy expenditure. Stress is the response of the system to the stressor. Responses to stressors may include adaptation or functional disorder. Adaptations allow the system to overcome the stress or to avoid it. Functional disorders can be ameliorated or can eventually lead to exhaustion and death. H. T. Odum (1967) pointed out that, although different stressors had different impacts on an ecosystem (e.g., removal of organisms, higher respiration rates, or diversion of incoming resources), they all diverted potential energy flows that otherwise could do useful work in the system. He then defined stress as a drain of calories of potential energy flow. According to his definition, stress can be measured by changes in the flows of energy in a system, disappearance of previously existing flows, or acceleration of repair work.

TYPES OF STRESSES AND STRESSORS

Regardless of how stress is defined or of the stressor involved, the concept of stress as normally used invokes an interference with the normal function of a system; its effects are most dramatically observed after certain thresholds of tolerance are exceeded; and it appears that beyond these thresholds recovery is usually difficult. When systems are stressed for short periods of time and have an opportunity to recover during periods of low stress, the stressor is said to be acute. Other systems are exposed to the effects of continuous or chronic stressors. When organisms function despite the presence of a chronic or acute stressor, the intensity and the type of stressor are said to be adaptable because they allow the systems to survive. Surviving systems are equipped to overcome the drain of potential energy and still remain competitive. Adaptability does not imply absence of an energy drain, however. All stressors are analogous to energy barriers that organisms and ecosystems must continuously overcome if they are to survive. For example, a halophyte must constantly deal with the problem of salinity even if it is adapted to salinity, just like wetlands and certain forests must overcome flooding or fire even though they have adaptations to cope with these factors. Morowitz (1968) said that the rate of protein turnover in organisms follows an exponential function of temperature which rises rapidly above 40°C for most animals. Thermophilic bacteria, however, can survive higher temperatures because their

rapid rise in protein turnover occurs above 50°C. The cost of high-temperature survival in terms of protein synthesis is staggering, however, and only a few species with very low biomass and a fast turnover of this mass can survive such conditions. If the pH of the water changes, then an aquatic organism's tolerance to high temperature decreases (Brock, 1970), presumably because of a synergistic effect of one stressor on another (Vernberg and Vernberg, 1974).

Thus it appears that we need to distinguish between the stressors that are part of an ecosystem's "normal" everyday environment and those added by man or by acute events with infrequent recurrence. Both types cause energy drains, but the effects of natural stressors are not as immediately obvious to an observer as are those of additional energy drains imposed allogenically on a system.

ENERGY COST OF STRESS

The energy cost of stress to a system is probably a function of the intensity of the stressor (i.e., how much energy it drains per unit area and unit time), the multiplicative or additive effect of this energy drain on the overall function and homeostasis of the system, the frequency of its occurrence, the type of ecosystem being stressed, the condition of the system at the time of impact, the intensity of other stressors at the time of impact, the residual effects of other stressors on the system, and the frequency of return of these particular stressors. Chronic stressors, which operate for longer time periods than acute stressors, usually drain more energy from a system. Acute stressors may be very damaging, however, depending on the intensity of the stress, the time interval at which it reoccurs, and the adaptability of the stressed system. Also, the multiplicative impact of energy drains on the overall function and homeostasis of the system deserves careful consideration since a small energy drain in a component with large amplification value on the function of the ecosystem may be more damaging than a large energy drain in one with less influence on other properties of the system. An example would be the relative impact of a poison vs. that of a fire on the growth of an ecosystem.

PREDICTABLE AND UNPREDICTABLE ENVIRONMENTS

Some investigators have differentiated environments on the basis of predictability and used this difference as a measure of stress (Slobodkin and Sanders, 1969; Sanders, 1969; Colwell, 1974). They

give as examples of unpredictable environments boreal and tropical sea bottoms with low dissolved-oxygen concentrations (< 2 to 5% saturation) and seasonal temperature fluctuation (~5.5°C), sewer outfalls and outfalls of canneries, the edges of anoxic zones in estuaries and lakes, and deserts. Hickman (1975) considered the shallow soils of the upper slopes of mountain peaks to be unpredictable environments for plants growing on them. Bleakney (1972) suggested that acyclic extreme tides prevented the occurrence of genetic selection and behavioral adaptation in littoral communities. Ehrlich et al. (1972) documented the extinction of butterflies and the lowering of population densities in subalpine ecosystems as a result of unusual weather (a wet June followed by heavy, late snows).

These environments are obviously harsh, with factors that exhibit a relatively wide amplitude of variation, but are they really unpredictable? Slobodkin and Sanders (1969) defined an unpredictable environment as one in which "the variance of environmental properties around their mean values are relatively high and unpredictable both spatially and temporally." This definition is subjective and presents a few problems when it is used to evaluate the degree of unpredictability of natural environments. First, data are usually meager and do not allow the necessary calculations. Second, seasonal variations may appear to be unpredictable when they are, in fact, very predictable over a longer period of observation. Third, how do we know what is unpredictable to a natural system? The problem with the use of the terms predictable and unpredictable was made obvious in the discussion following the presentation of the paper by Slobodkin and Sanders at the Brookhaven symposium in 1969. Slobodkin could not agree with L. C. Cole on whether cave, hot-springs, and salt-lake ecosystems were or were not predictable environments. Yet, we would intuitively consider them very stable environments. In fact, Brock (1970) showed this to be true for hot springs, and Poulson and Culver (1969) described the environmental constancy of the cave environment.

Colwell (1974) conceptualized the term predictability as the sum of two separate components, constancy and contingency. Contingency represents the degree to which time determines a state (the value is minimal when the probability of occurrence of each state is independent of season), and constancy is a measure of sameness of state from year to year. Predictability, according to Colwell, is essentially a measure of the variation among successive periods in the pattern of a periodic phenomenon. When the variation is low, predictability is high. He argues that the same degree of predict-

ability can have different effects on different organisms and that constancy and contingency may be as important as elements of adaptive strategies as they are as environmental constraints on evolution.

Since predictability implies anticipation, predictable environments can be anticipated, but unpredictable environments cannot. The ability to anticipate rests on the system subjected to the environment; thus the relationship between the system and its environment becomes crucial in defining the degree of predictability or unpredictability an environment represents to a system. Slobodkin and Sanders (1969) said that predictability was partly dependent on the organism and was not necessarily an environmental property. We would expect that, all other conditions being equal, the smaller and simpler the system, the greater its susceptibility to short-term environmental variability. However, miniaturization may be a successful evolutionary response to a long history of wide fluctuations. Regardless of strategy, if we assume that survival implies adaptability and that adaptability enhances anticipation of the environment, we would call the same environment an unpredictable one for the system that perishes and a predictable one for the system that survives.

Environments have also been described as constant, inconstant, cyclic, and randomly fluctuating or as being in any intermediate state. Stearns (1978) showed that it is incorrect to think in terms of just two contrasting situations (predictable or unpredictable). He found that even within one type of ecosystem (reservoirs) analysis of four variables separated 19 of them into distinct classes of variation that formed a diverse mosaic of environments. Stearns concluded that different environments could rank differently for any measure of fluctuation or stability for each significant environmental variable. Whittaker (1975) pointed out several possible characteristics of fluctuations that need consideration—quality and duration, relative amplitude of a regular fluctuation, relative irregularity, and duration of the pattern in evolutionary time. Obviously the number of points along a continuum of possible intensities of stress associated with these types of environmental situations is significant to any analysis of stress and ecosystems.

The classification of an environment in any category depends on our ability to analyze and understand data and on the completeness of the data sets. Complex time-series analyses are required to detect long-term cyclic events on data sets that before analysis appear to be random and unpredictable. The long-term cycles, although perhaps not important to organisms, may be significant to populations or

whole ecosystems, as shown, e.g., by Stearns (1975) in his discussion of the effects of reservoir fluctuations on the evolution of populations of mosquitofish. Analyses of this type are becoming very common in the literature (Colwell, 1974; Sneyers, 1976; Dyer and Tyson, 1977). Findings indicate that such potential stressors as drought (Dyer and Tyson, 1977), fire (Houston, 1973), hurricanes (Thomas, 1974; Gentry, 1974), flash floods (John, 1964), storms that cause catastrophic drifts (Anderson and Lehmkuhl, 1968), or rainfall (Beatley, 1974; Colwell, 1974) have recurrent, predictable patterns to which ecosystems can adapt and which they depend on for their survival and maintenance.

Living systems "track" the environment through a number of adaptations that have bearing on environmental anticipation, e.g., storages of energy, life forms, strategies of life cycles, phenological patterns, migrations, successional recovery, alterations in rates of physiological processes, and lowering of productivity-to-biomass ratios. At the population level, e.g., Bott (1975) showed that bacteria in a stream with a fluctuating thermal event (up to 23°C/year) had adapted to a temperature 5 to 20°C higher than the mean temperature of the stream. An optimum growth temperature near the lethal temperature becomes a predictive mechanism for random temperature fluctuations; temperature increases have less likelihood of exceeding the higher tolerance limit.

Environmental fluctuations are stressful to ecosystems (Dunbar, 1960), and, as the environment becomes more variable, the cost of anticipation should increase. Anticipating a changing environment remains an essential prerequisite of life, however, if the organism or the ecosystem is to survive.

I agree with Margalef's idea (1969; 1975) that, as they develop toward the steady state, ecosystems gain information that, in part, allows them to anticipate fluctuations in their environments. At the ecosystem level an event may cause mortality in certain sectors of the system, but the system as a whole may be able to adapt to it. For example, hurricanes kill mangrove trees, but they are essential for the survival of the mangrove forest (Cintrón et al., 1978). The annual migration of the thermocline in a temperate dimictic lake creates severe problems for certain populations of bacteria, zooplankton, and phytoplankton, but, for the lake as a whole, this event is predictable and essential for the distribution of heat, nutrients, and organic fuels. Thus, if we select the whole ecosystem as a point of reference, there cannot be naturally unpredictable environments that are colonized by steady-state ecosystems. Harshness of the environment should not be confused with unpredictability.

Truly unpredictable events are, perhaps, earthquakes and many human impacts. Human interferences with natural ecosystems are unpredictable because they do not necessarily follow a recognizable pattern and they do not operate long enough to allow for adaptations to develop. Many activities of man, while nonadaptable for many natural systems, however, do select for interface ecosystems that quickly adjust to human interference and develop short-term steady states depending on continuous human intervention. These systems have many of the characteristics of the physically controlled communities described by Sanders (1969, Table 1) and are dominated by exotic or successional species.

TABLE 1

PROPERTIES OF PHYSICALLY CONTROLLED, BIOLOGICALLY ACCOMMODATED, AND STRESSED ECOSYSTEMS*

Physically Controlled
Small numbers of species per numbers of individuals
Widely fluctuating physical conditions that are not rigidly predictable
Organisms exposed to severe physiological stress
Environment of recent past history
Biologically Accommodated
Large numbers of species per numbers of individuals
Physical conditions constant and uniform for long periods of time
Environment of high predictability
Ecosystems Under Stress
Succession arrested or set back periodically
Few successional stages between pioneers and climax; autosuccession and cyclic succession common
Plants may show stress by aberrations or leaf deformations
Changes in the intensity of stressors cause shifts in species composition; generally species diversity decreases with successional time
P/R ratios of 1, >1, or <1 at steady state
Speed of succession is a function of physical environment and the point in the system where disordering energies act
Species show zonations that reflect gradients of stress; zones should not be confused with successional stages

*Data on "physically controlled" and "biologically accommodated" ecosystems are from Sanders (1969).

ENERGY BASIS OF STRESS

H. T. Odum's (1967) definition of stress as a drain of potential energy has an advantage over all other definitions because it provides a common basis (energy) on which to evaluate all types of stress in all kinds of systems. More significant, however, is that the energy required for all natural processes behaves according to well-defined laws that provide a quantitative basis for evaluating ecosystem function and response to stressors. The capacity of a system to overcome stress, then, depends on the balance between the rate of recovery of its energy stores and the magnitude of the energy drain caused by the stressor.

We could argue against Odum's definition of stress by pointing out that many drains of potential energy are not normally called stress but would be by his definition, e.g., the energy drain of nighttime respiration in plants. We would not normally identify nighttime darkness as a stressor, but shading of a plant or an ecosystem for a prolonged time period certainly would be considered one. Rogers (1977), for example, after shading a coral reef for 35 days, found significant rates of mortality and slow rates of recovery.

The health of ecosystems that are normally considered highly stressed could also be used to illustrate the futility of identifying stressors and defining what they do to a system. Salt springs, thermal springs, or deserts actually become stressed if the "stressful conditions" to which they are adapted are changed. The usefulness of the concept of stress is obviously limited if we cannot deal with the apparent subjectivity and relativity of the term.

Selye (1956) suggested that most environmental situations can become stressful to given individuals and that stress is a normal condition of anyone's environment. The realization that stressors and energy drains are part of any natural environment is an important step in generalizing about stressors and their impact on ecosystems. This is the basis for my earlier suggestion that we differentiate between background or normal stress and additional stress caused by allogenic forces. In fact, as discussed in the following section, stressors may become subsidies to certain ecosystems, and their productivity and growth may decrease if the stressors are removed (Fig. 1).

Push–Pull Model of Stress

Figure 2 is a model of the push–pull (positive–negative) effect of ordering and disordering factors in the environment (in this case, temperature) proposed by H. T. Odum (1974). The model depicts

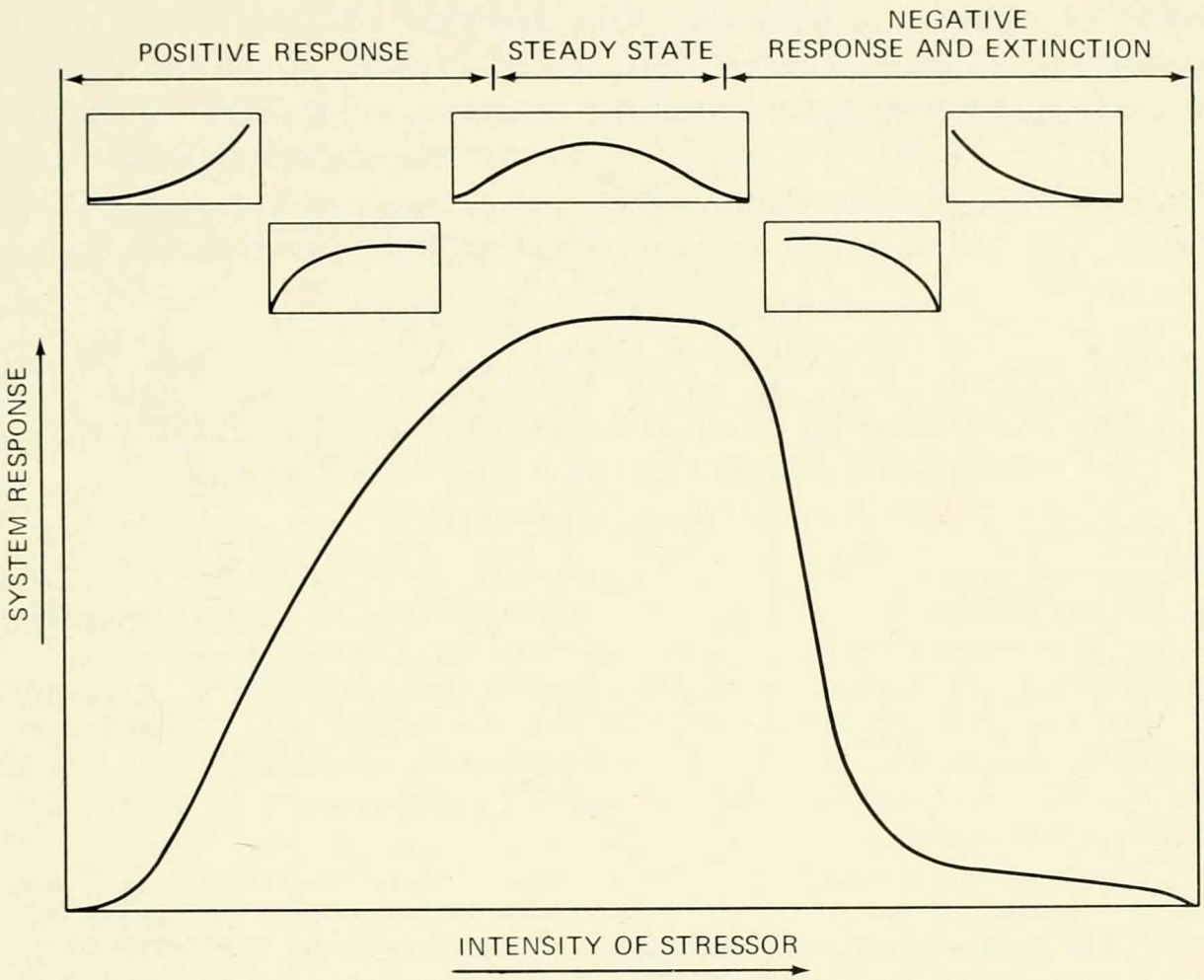

Fig. 1 Response of living systems to stressors. Similar curves of response were proposed by E. P. Odum (1971), Gibbons (1976), and Odum and Kroodsma (1976). Examples of positive response with increasing stress intensity were reported by Yentsch et al. (1974) for algal populations under temperature stress and by Carpelan (1964) for algae under salinity stress. Conditions of steady-state response are common in most stress experiments [e.g., Woodwell and Rebuck (1967) for radiation and Erdman (1966) for DDT and X rays]. Rapid declines and extinction are equally common (Woodwell and Marples, 1968; Coutant and Cox, 1976). Few studies cover the whole spectrum of response for a given environmental factor.

the well-known facts that all structures have a natural tendency to deteriorate and that life as we recognize it represents an improbable state of organization whose maintenance requires continuous energy flows. The implication is that certain drains of potential energy that we call stresses when they irreversibly alter a system are, in fact, necessary and constantly present components of all life processes. H. T. Odum (1976) suggested that disordering stimulates ordering and, thus, questioned the tendency to regard stress as bad and disorder as evil.

The push—pull model of stress proposes that stressors, such as temperature, may initially accelerate and then decelerate processes.

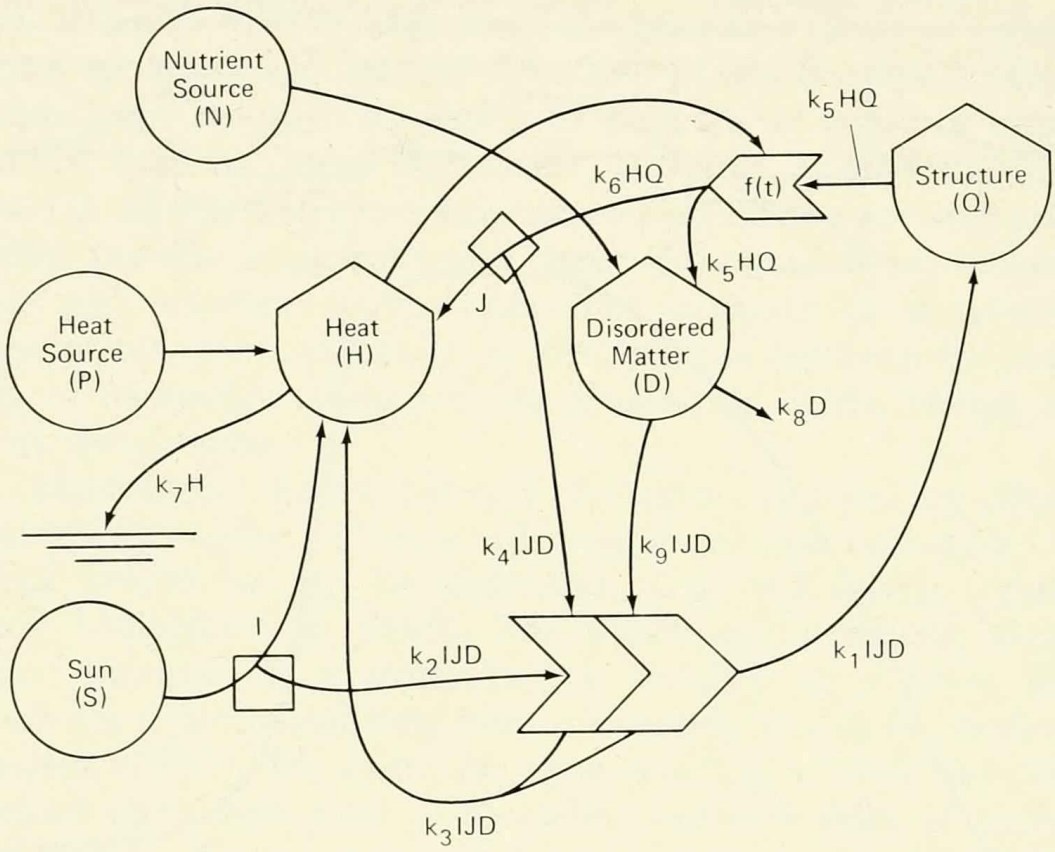

Fig. 2 Model of push—pull effects of thermal energy on ecosystems proposed by H. T. Odum (1974). Note that ordering and disordering processes depend on each other. Arrows show the direction of energy flows; tanks are state variables; the large double arrowhead represents multiplicative energy interactions; and the circle represents the energy source.

Depending on the characteristics or state of the stressed system, the energy influx of the stressor may or may not benefit the system. H. T. Odum (1974) pointed out, for example, that high-temperature stress may be useful in accelerating rates of respiration, thus causing the release of minerals for photosynthesis. This function would be a positive asset to an oligotrophic aquatic system but not to a eutrophic system. Nixon (1969) and Odum, Nixon, and DiSalvo (1970) postulated a similar role for photorespiration in oligotrophic hypersaline systems rich in organic matter. In this case, the energy drain of photorespiration was shown to benefit mineral availability in an otherwise nutrient-poor system. Disruptive stressors, such as fires, tides, floods, water currents, volcanic eruptions, and hurricanes, also have a positive role at the ecosystem level. Without a periodic disruption ecosystem growth processes stagnate as resources are immobilized by their structure. Bursts of growth and high net productivity usually follow disturbances, and rejuvenated systems replace senescent systems. To have a positive effect, the energy input

to a system must be coupled with increased availability of other essential resources. Otherwise the input energies cannot be usefully converted. Table 2 summarizes literature examples of push—pull effects of different stressors.

These examples suggest that, as the inputs of energy to a system change (including energies that push and/or pull), the biotic

TABLE 2

EXAMPLES OF POSITIVE (PUSH) AND NEGATIVE (PULL) EFFECTS OF STRESSORS ON ECOSYSTEMS AND POPULATIONS*

Stressor	Pushing effect	Pulling effect
Ionizing radiation	Observed faster decomposition, leaf fall, growth, and recovery rates for a variety of dosages (Woodwell and Marples, 1968)	Can be lethal; disrupts structure and increases respiration rates; changes species composition (Ferens and Byers, 1972)
Tidal extremes	Redistribute nutrients, sediments, organic matter, and organisms (Odum, Copeland, and McMahan, 1974)	Exposes organisms to lethal conditions (Glynn, 1968)
Water flow	Brings nutrients and redistributes larvae (Anderson and Lehmkuhl, 1968); brings food and O_2 and removes toxic substances (H. T. Odum, 1955)	Removes structure; causes high energy maintenance costs in plants and animals (Anderson and Lehmkuhl, 1968; Moore, 1964)
Flooding	Removes competition; signals the beginning of phenological events (John, 1964)	Increases energy maintenance costs; temporarily decreases number of taxa and individuals (Hoopes, 1974)
Volcanic eruptions	Allow for better nutrient, moisture, and competitive environments (Eggler, 1967)	Suffocate and kill plants and animals (Eggler, 1967)
Denudation, clipping, herbivory, or defoliation	Stimulates plant productivity (Churchill et al., 1964); diversifies community at low rates (Penfound, 1964)	Removes structure and reduces diversity at high rates; causes mortality (Churchill et al., 1964)
Salinity	Allows higher gross productivity in mangroves up to about seawater strength (Hicks and Burns, 1975)	At values higher than 35‰, increases respiration rates and decreases transpiration and net productivity rates (Lugo and Snedaker, 1974)

(Table continues on following page.)

Table 2 (Cont.)

Stressor	Pushing effect	Pulling effect
Eutrophication	Stimulates primary productivity and growth of consumers (E. P. Odum, 1971)	Shifts species composition, causes anoxic conditions, and eventually reduces species diversity and complexity (E. P. Odum, 1971)
Fire	Makes nutrients and moisture more available; reduces competition (Wright, 1976)	Removes structure (Wright, 1976)
Herbicides, oil, and other poisons	Select for certain life forms over others, survivors grow faster (Wein and Bliss, 1973; Niering and Goodwin, 1974; Burk, 1977)	Reduce productivity by altering behavior and physiology, poisoning, and killing organisms (Krebs and Burns, 1977); lowers species diversity (Tomkins and Grant, 1977)
Heavy rains	Act as a clue for starting phenological events in deserts (Beatley, 1974); relieve salinity in coastal situations and redistribute nutrients (Chabreck and Palmisano, 1973)	Remove structure and may cause other stresses, such as flooding, which affect gas exchange of wetlands sediments and the turbidity in aquatic systems (Hoopes, 1974)
High temperature	Accelerates processes, particularly respiration and recycling (Smith et al., 1974)	Can be lethal; reduces species diversity (Kullberg, 1968)
Low temperature	By slowing down processes, allows for conservation of storages (Mooney and Billings, 1965)	Freezes can be lethal
Temperature amplitude	If short-term, fluctuations may stimulate metabolism (Sweeney and Schnack, 1977); increases resistance to thermal shock (Hubbs, 1964)	If amplitude is wide and change is rapid, it can be lethal (Hubbs, 1964; Sastry, 1976)
Hurricanes	Bring water, nutrients, sediments, and propagules (Chabreck and Palmisano, 1973)	Structure is removed (Craighead, 1964)
Insecticide	DDT (5—10 ppm) enhances resistance to X-ray radiation (Erdman, 1966)	Eventually lethal (Erdman, 1966)

*Literature citations are not intended to imply that these are the only or the most significant documentations of the example.

components selected for are those that somehow maximize energy flow despite the presence of stressors. This is done either by diverting all incoming energies to overcome stress or by extracting useful work from the disordering force. Energy drains are normal processes affecting living systems and should be identified as such even if they normally do not reach critical thresholds beyond which recovery is difficult.

To evaluate the relative impact of push—pull effects on ecosystems and to gain insight into the cost of recovery and ecosystem resilience, we can calculate ratios of disordering-to-ordering energies (Richey, 1970). This involves calculating the magnitude of energy

TABLE 3

RATIO OF DISORDER TO ORDER IN ECOSYSTEMS SUBMITTED TO STRESS

Ecosystem	Stressor	Disorder/order	Reference
Subtropical dry forest	Cutting	1 : 1,270	Ewel, 1971a
Subtropical dry forest	Herbicides	1 : 17	Ewel, 1971a
Subtropical moist forest	Gamma radiation	1 : 10,000	H. T. Odum, 1970
Microcosms (terrestrial)	Burning	1 : 13	Richey, 1970
Microcosms (aquatic)	Sonication and temperature	1 : 10,000	Richey, 1970
Vietnam (whole country)*	War (including bombs and herbicides)	1 : 8.7	Brown, 1977

*Reduced to fossil fuel equivalents.

flows that disrupt ecosystem structure and function and the magnitude of energy costs associated with reordering and maintaining order in the system. Table 3 summarizes literature reports on this ratio. Most values are derived from experimental situations, where the disordering input can be computed easily. Results show that disordering energies have considerable amplification and that building and maintaining order is extremely expensive relative to the cost of destruction. Obviously, the capacity of a system to regenerate depends on the availability of enough energy sources to reorganize the disordered structure. Since the availability of energy is a function of the environment, the type of environment dictates rates of recovery and degree of complexity at the steady state. In the term complexity, I include such measures of ecosystem organization as

species diversity, structural organization, physiognomy, and phenological organization.

The concept of stress should, then, be applied in a hierarchical fashion relative to the various levels of biological organization. As ecologists, we are interested in stressors as they relate to life zones, individual ecosystems, and populations. Other scientists do their analysis at the organismal, cellular, or molecular and atomic levels of organization. To avoid the pitfalls of subjectivity, we need to develop appropriate criteria for evaluating the relative effects of stressors on the complexity and rate of recovery of systems at each of these levels of organization.

The Energy Signature of Ecosystems

The push—pull model (Fig. 2) suggests that the amount of structure and complexity a system is capable of building and maintaining depends on the net effect of positive and negative forces in the environment.

The sum of all incoming energy flows to a system and the pattern of their delivery expressed on an equal energy-quality basis is called the "energy signature" of the system (H. T. Odum et al., 1977). The quality of an energy source depends on its concentration (Odum et al., 1977). High-quality sources have a high energy content per unit volume, and low quality sources, like solar energy, are diluted and, thus, perform less work per unit volume. Energy signatures must be expressed on an equal energy-quality basis to show the relative ability of the components to generate work and control the system. The energy signature provides a way to categorize ecosystems according to environmental carrying capacity or capacity to deal with stress, e.g., as Odum, Copeland, and McMahan (1974) did for coastal systems. As the energy signature changes, the loss or gain of energy may become a source of stress or a subsidy to the system.

Since the actual intensity of background or normal disordering energies in a given environment may be impossible to measure, the measure of stress at the level of the life zone must be made relative to the most complex systems on earth, because they represent the best that can be done with the energy flows and resources available to all natural systems. Other life zones could then be arranged in a hierarchical and relative scale.

Perhaps the best system for classifying terrestrial and wetland ecosystems is Holdridge's life-zone system (1967) (Fig. 3). This system has worldwide application, is an objective determination of life zones based on climatic data (which approximate the energy

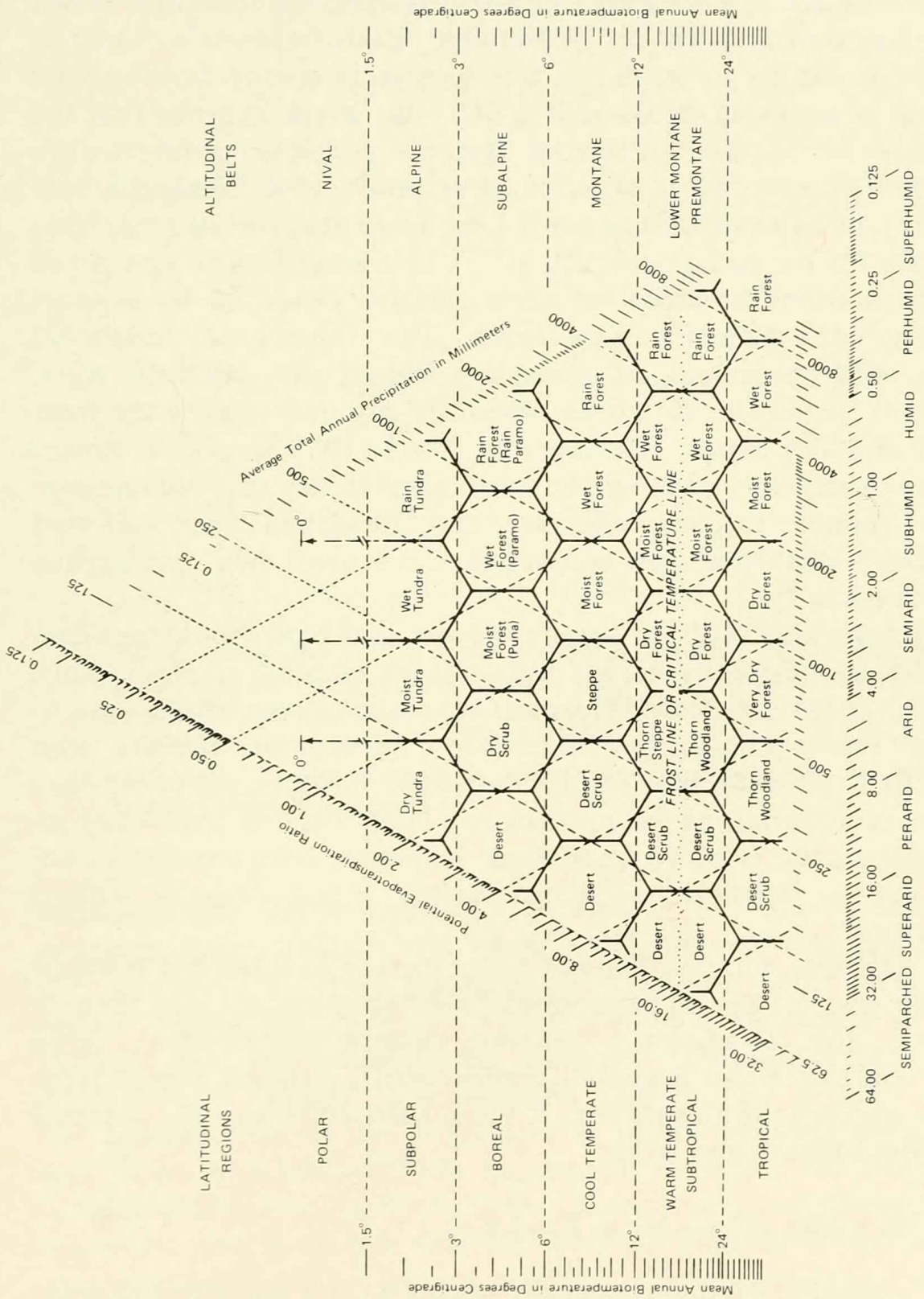

Fig. 3 Life zone classification system of Holdridge (1967). Each life zone is characterized by a specific energy signature that determines its potential to support ecosystem complexity.

signature), attempts to account for the factors that control ecosystem productivity, and has been tested widely (Holdridge et al., 1971). The life zone is a bioclimatic zone of the earth with a unique set of conditions and capacities to support biological complexity. For each climatic life zone of the world (Holdridge identifies about 120), a maximum level of ecosystem performance is possible. Performance can be measured in terms of gross energy flow or total ecosystem complexity. Holdridge (1967) has already shown that the complexity of forested terrestrial systems varies according to life zone. This complexity is equal to the product of maximum tree height (m), number of species per 0.1 ha, basal area (m^2 /0.1 ha), tree density per 0.1 ha, and a constant, 10^{-3}. Life zones can be compared with one another in terms of their relative potential to support ecosystems of different complexity. The impact of additional stressors on a given type of ecosystem should vary with life zone. Ecosystems in humid life zones obviously respond differently from those in arid life zones. For example, Ewel (1977) reported slower responses to stressors (cutting and herbicides) in dry tropical climates than in humid tropical climates and described two different successional strategies for ecosystems in these two contrasting environments.

His results and those of others suggest that care should be taken in comparing ecosystems across latitudinal or climatic gradients since they should not be expected to exhibit the same speed of response to stressors. The optimism of Slobodkin and Sanders (1969), who suggest that latitude has no fundamental importance on species diversity considerations, is premature. They believe that environmental constancy is more important; however, environmental constancy per se, without adequate energy inputs, cannot sustain complexity.

The life-zone concept has not been applied to lakes and streams, but these systems are so dependent on external inputs that there is no reason not to expect a life-zone pattern within them. Since climate controls water availability and runoff, nutrient runoff from the land, and evapotranspiration, it should also influence the patterns of response of lakes and rivers.

Model of the Action of Stressors on Ecosystems

The analysis of individual ecosystems requires detailed examination of the forces acting on them. To analyze the possible ways in which stressors affect individual ecosystems, I first develop a conceptual model of an idealized unstressed ecosystem (Fig. 4). In this simple model, we can see the relationship between four state

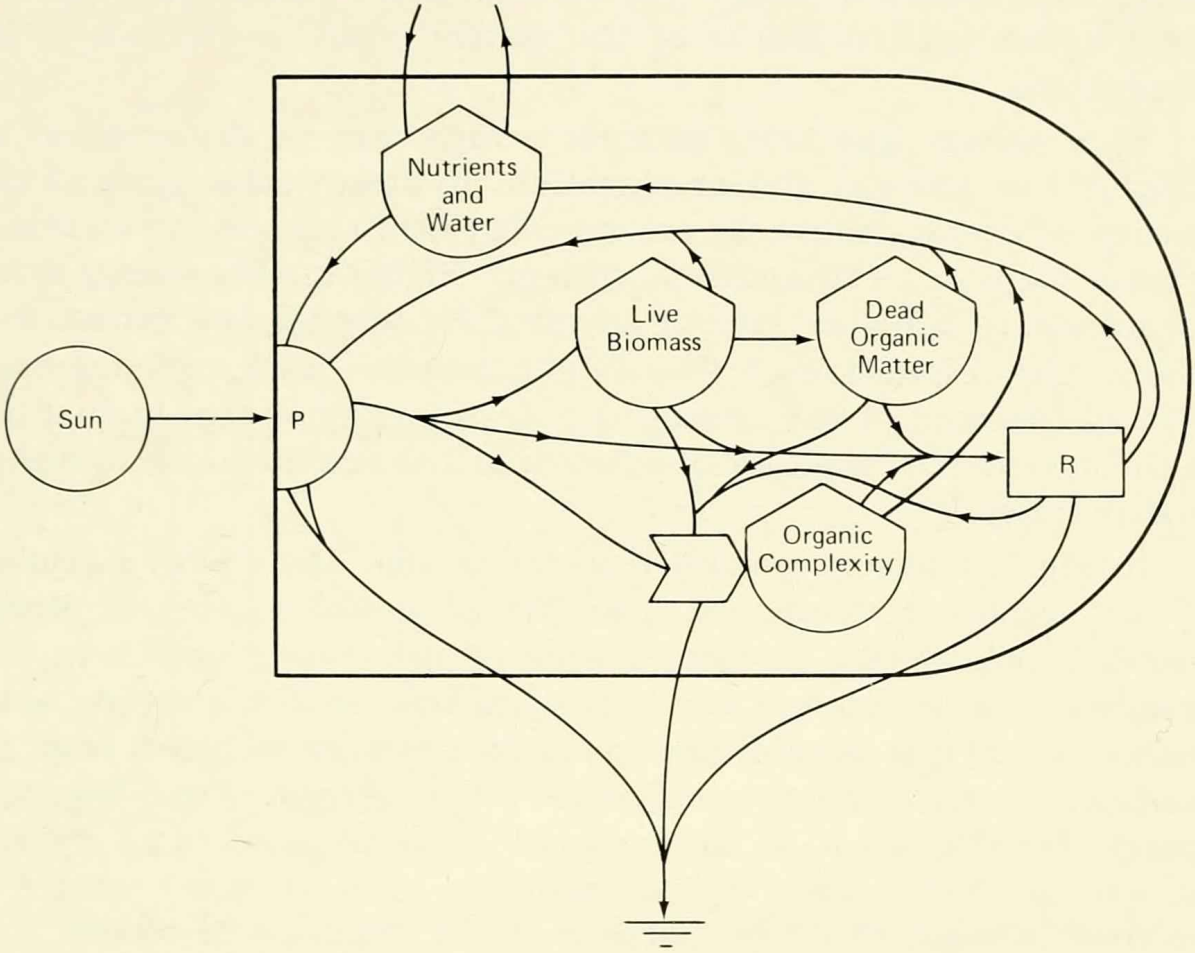

Fig. 4 Simplified model of an ecosystem without stress. The large bullet-shaped outline is the boundary of the system; P is photosynthesis; and R is respiration (for other symbols, see Fig. 2, and, for a discussion of the model, see the text). All energy inputs are eventually dissipated into degraded heat, according to the second law of thermodynamics.

variables and three ecosystem processes. The state variables are nutrient concentrations and water availability (a measure of fertility), live biomass, dead organic matter, and a hypothetical variable called organic complexity, which includes measures of species diversity and three-dimensional diversity and complexity discussed by Whittaker (1969). It is included here simply to point out that the organization of the ecosystem is an energy-demanding process and, thus, is subject to the impact of stressors. The cost of this variable is borne by each of the living components of the system, but this does not invalidate the fact that complexity of function and organization is an ecosystem property that responds to its energy signature. All state variables have a positive role in the system and provide positive feedback to its productive sector. The processes illustrated in the model are the photosynthetic conversion of solar

energy into chemical energy (P), the respiratory process (R), and the many cycles and feedbacks of the system which contribute to its homeostasis.

In a system like this, there is a high cost of depreciation to support live biomass and organization. In steady-state systems the quality of energy feedbacks among ecosystem components increases relative to those of successional systems. Higher quality energy flows contribute to a higher rate of energy flow through the system as a whole. The respiration of the system increases on a unit-area basis with age because of the increasing cost of upgrading energy qualities in the system (i.e., the cost of converting low-quality forms to higher quality states).

In Fig. 5 stressors are added to the model. The energy signature of the system is subdivided into five potential sources of stress. Source 1 delivers the primary energy of the system, which in this example is solar energy for photosynthesis; source 2 diverts solar energy before it is transformed to chemical energy by plants (e.g., by shading); source 3 diverts energy after it is transformed into chemical energy but before it is incorporated into structure (e.g., by the harvest of labile sugars by a consumer, such as man); source 4 removes storages (e.g., by harvests or by drainage of water); and source 5 accelerates the respiration of the system (e.g., by changes in temperature). Each of these external sources impinges on the ecosystem at a certain rate and with a certain periodicity of delivery which depends on the type of life zone. When the energy signature changes, the change may become stressful.

The model of stress in Fig. 5 suggests that different stressors affect different functional sectors of the ecosystem and that perhaps the response of the system to these different types of drains also changes according to the type of stressor. Causal relationships must then be analyzed relative to the type of stressor, its pattern of delivery, its intensity, and the kinds of changes that it causes in the system. After a certain threshold is exceeded, the stressor causes energy flows to be diverted away from the system and diminishes the ability of the system to continue to upgrade internal energy stores. Thus the overall organization and homeostasis of the system is altered. There is flexibility in each system, however, with regard to its response to and the ultimate impact of the stressor. According to Fig. 5, more energy may be diverted into living mass, less into complexity, or more into respiration, or there may be an increase in the amount of dead organic material. The ultimate strategy probably depends on the type of stressor and where in the system it operates.

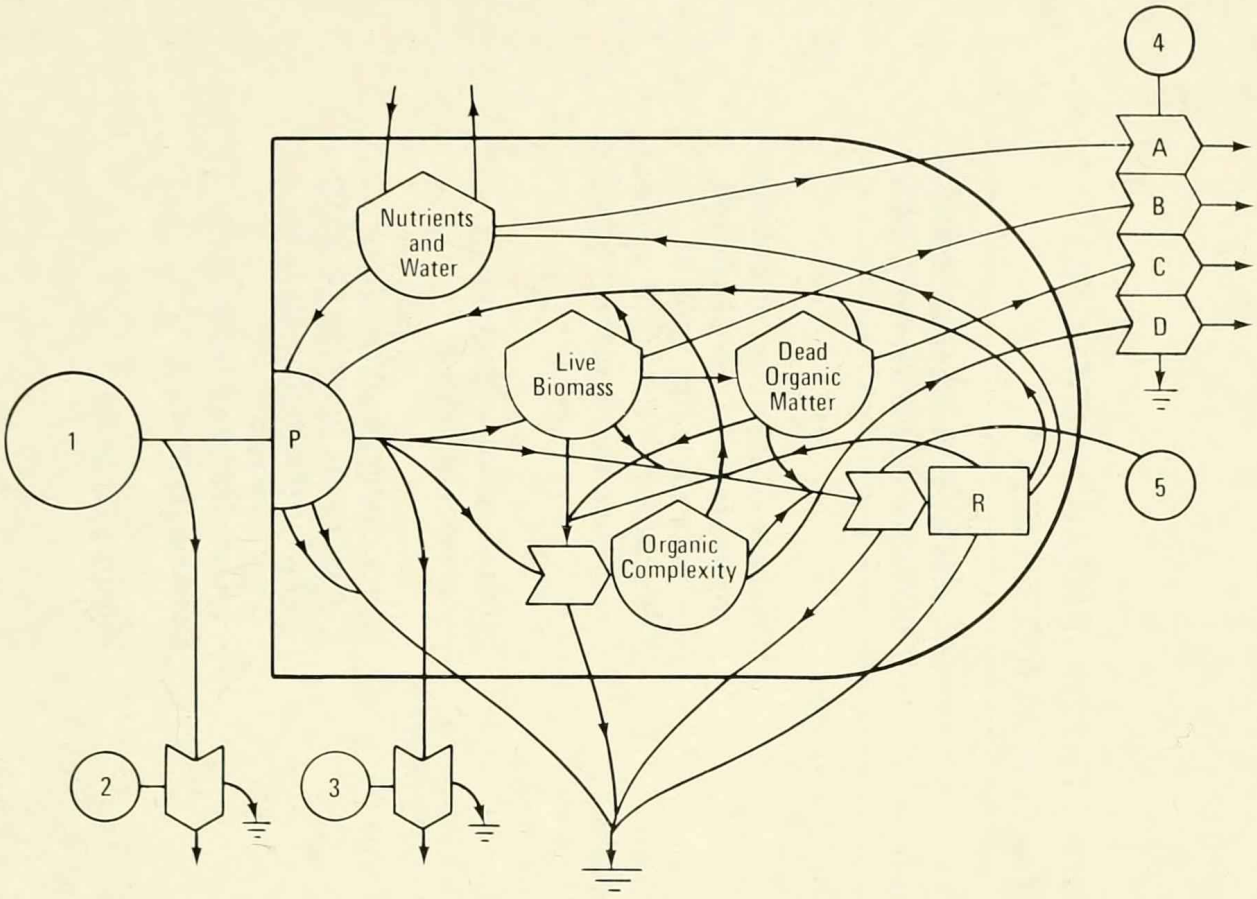

Fig. 5 Simplified model of an ecosystem influenced by a number of stressors. (For identification of symbols, see Fig. 2, and, for a discussion of the model, see the text.) Each stressor, by draining energy from a different sector of the ecosystem, affects the response in a unique way. Stressorr 4A, for example, has a stronger effect on the system than stressors 4B or 4D because it directly affects the photosynthetic process and, thus, decreases the ability of the system to restore its energy stores. Stressors 1 to 3 are equally damaging to ecosystems relative to the effects of stressors 4B to 4D and 5.

The point we need to emphasize is that, although all stressors divert potential energy away from the system, not all stressors handicap the system to the same degree, even though they drain equal amounts of energy. For example, a stressor that removes structure but does not alter the primary productivity of the system may not have as much impact as one that reduces the ability of the system to photosynthesize and, thus, to replenish its energy stores. In the first case the system will recover rapidly, but in the second recovery may be slow. This aspect of the problem has important implications for rates of recovery from stress and for management of natural ecosystems. Table 4 lists a number of naturally stressed ecosystems and classifies their respective natural stressors by type. I have tried to illustrate the rate at which the systems respond to stress

TABLE 4

EXAMPLES OF HOW THE POINT OF ACTION OF STRESSORS (ACCORDING TO FIG. 5) AFFECTS THE RATE OF ECOSYSTEM RECOVERY*

Ecosystem	Natural stressor	Natural or experimental stressors that slow down recovery rates
Ecosystems with Fast Rates of Recovery		
Mangroves and salt marshes (Lugo and Snedaker, 1974; Cintrón et al., 1978)	Salinity (type 5)	Drainage or blocking of nutrient input (type 3), very high soil salinity (acts like type 3)
Florida sand pine scrub forest (Laessle, 1958)	Low fertility (type 3) but recovers after fire (type 4) which makes nutrients available in mesic environment	Elimination of fire or of nutrient recycling mechanisms (type 3)
Eutrophic waters (Wetzel, 1975)	Low oxygen (type 3 or 5), high water-flow rates (type 4), or no water flow (type 3 or 5)	Intensification of natural stressors of type 3
Riverine swamps (Gardner et al., 1972)	Intermittent floods (type 5)	Either drainage (type 4A) or continuous flooding (type 5), which eventually cuts plant translocation (type 4A) and lowers leaf-area index (type 2)
Springs, rivers (H. T. Odum, 1955)	Water flow (type 4)	Shading (type 2)
Coral reefs (Rogers, 1977)	High wave and water-current energy (type 4)	Shading (type 2)

Table 4 (Cont.)

Ecosystem	Natural Stressor	Natural or experimental stressors that slow down recovery rates
Ecosystems with Slow Rates of Recovery		
Granite outcrops and other arid ecosystems (Lugo and McCormick, unpublished)	Lack of water (type 3)	
Alpine and arctic ecosystems (Billings and Mooney, 1968)	Low temperature and lack of water (both act like type 3)	
Oligotrophic water (Wetzel, 1975)	Lack of nutrients (type 3)	
Bogs (Moore and Bellamy, 1973)	Continuous flooding by highly oligotrophic, low pH waters (types 3 and 5)	

*Stressors that reduce the ability of a system to photosynthesize and replenish energy stores slow down recovery rates more than stressors that act on other locations of the system. References provide relevant information on the particular ecosystems.

through successional recovery. Note that systems stressed by removal of structure or by acceleration of respiration can still function and will recover rapidly because there has been no direct impact on factors regulating primary productivity. Systems submitted to stressors that do alter their productive capacity, however, have little ability to recover or to negotiate further stress. If this is true, stressors affecting high-quality energy stores appear to have a lesser impact on a system than those affecting low energy-quality sectors of the system.

Change of Energy Signature

Examples of changes in the energy signature of an ecosystem are slow changes in climate (see Singer, 1970); changes caused in downstream sites by construction of a dam, e.g., the change in estuarine circulation patterns caused by the Aswan Dam (Sharaf El Din, 1977); and regional changes caused by alteration of water tables, e.g., in south Florida estuaries (Carter et al., 1973).

Cooper and Copeland (1973), experimenting with microcosms, simulated regional drainage changes for Trinity Bay in Texas. They found more changes in the respiration and productivity of the system than in species composition. Later, as stressors became more intense (simulated by lack of freshwater runoff or large organic-pollutant inputs), diversity index changed significantly and so did species composition. Alterations in energy flow rates before any significant changes in species composition were documented in the field by Carter et al. (1973). Apparently the substitution of species results from altered energy flows through the system. New ecosystem boundaries develop slowly in response to a different energy signature impinging on the ecosystem.

Under some circumstances a change in an energy signature could result in a new ecosystem, with higher complexity and productivity than the original system it replaced, e.g., the drainage of certain (but not all) wetlands, which creates mesic ecosystems. In this case the overall carrying capacity of the environment increases; the original ecosystem is selected against by the stressor; and the new system is more vigorous because it is better adapted to the new energy signature. J. Ewel (1978) documented such a succession in the Everglades of Florida.

Figure 6 shows as an example the energy signature of a marsh ecosystem subjected to thermal stress. It is obvious that, when energy quality is taken into consideration, tidal energy becomes the main energy source to a marsh, and fossil-fuel stress was not as significant as it appeared to be initially from its heat equivalence.

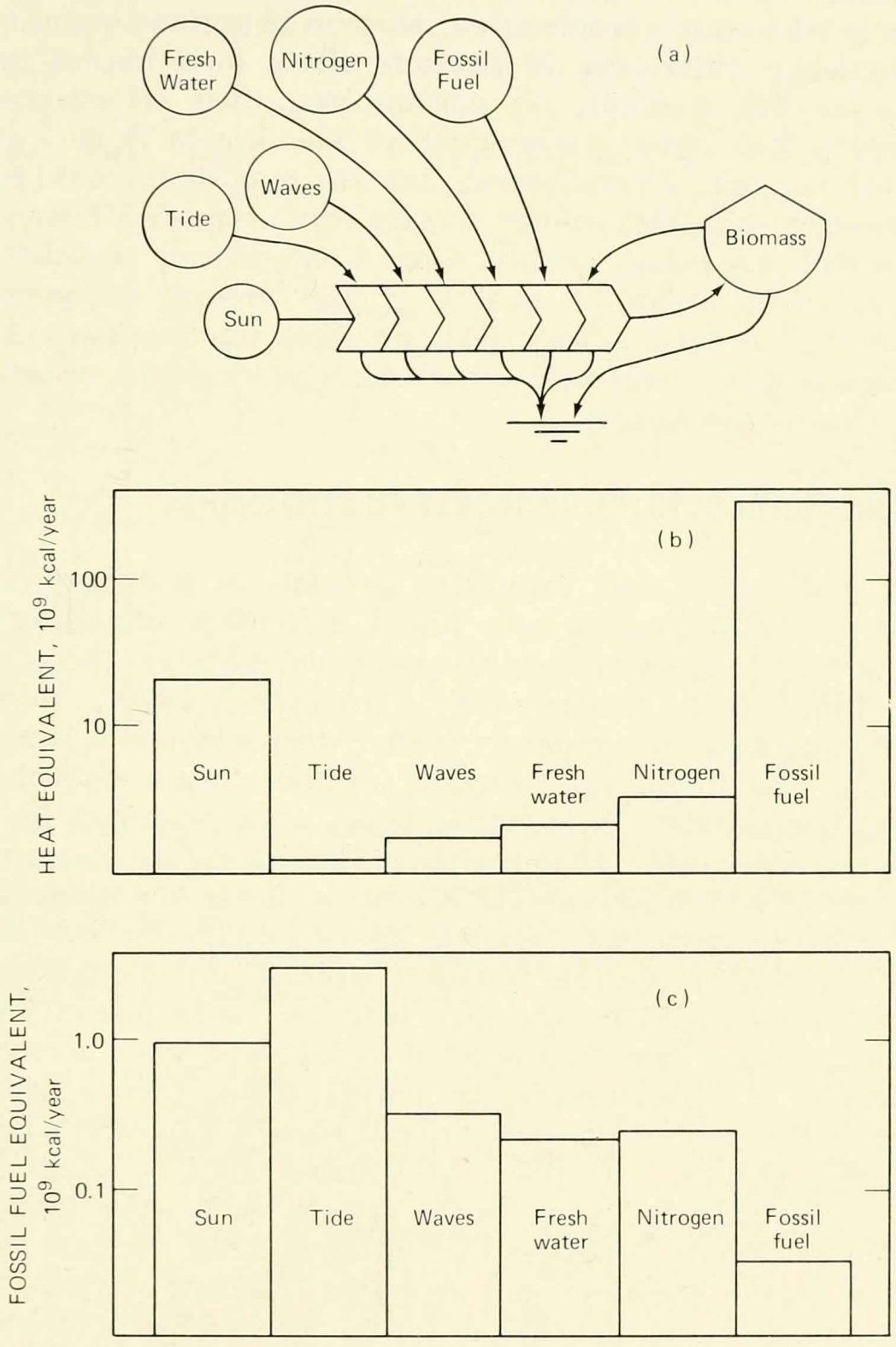

Fig. 6 Calculation of the energy signature of a marsh ecosystem under the influence of thermal pollution (a) [data from H. T. Odum et al. (1977)]. The symbols in (a) are described in Fig. 2. Note that, when all the energies are expressed on the basis of equal quality (fossil fuel equivalents), their relative importance (c) changes in comparison to calculations based on heat equivalents (b).

The change in the magnitude of an energy source when energy quality is taken into consideration raises an important question. Do energy-quality differences in stressors affect their impact on the ecosystem? For example, do poisons owe their effectiveness as stressors to their higher energy quality? The data in Table 3 do not allow for any valid generalizations, but the hypothesis could remain that stressors with high energy quality may be more effective than those with lower energy quality. Since I have already postulated the opposite effect when the quality of the stressed component is considered, it is possible that maximum stress results when a stressor with high-quality energy delivery affects a sector of the system with energy flow of low quality.

PATTERNS OF ECOSYSTEM RESPONSE TO STRESSORS

The response of cells, organisms, populations, and ecosystems to a wide variety of stressors may follow a common pattern (Fig. 1). This has been pointed out by a number of investigators (Selye, 1956; Platt, 1965; H. T. Odum, 1967; Woodwell, 1970), who also identified patterns of response. Usually, when a system is stressed, it overcomes the initial low intensity of the stressor by activating internal homeostatic mechanisms. These were described for cells, organisms, and populations by Selye (1956) and for ecosystems by Platt (1965) and Woodwell (1970). Many times low intensities of stress actually stimulate a system to performance above that of controls, probably because of higher internal physiological activity induced by the higher energy input (Fig. 1). As the intensity of the stressor increases, there is a period of steady state, when homeostatic mechanisms compensate for the energy drain, then a period of decline, and finally, if the stressor continues to intensify, a point of irreversible change. The point of collapse may be when energy reserves are exhausted or when the system reaches the limits of its adaptability. Figure 1 suggests that different stress response patterns reported in the literature may represent different sections of one single response curve that extends for the whole range of intensity of a given stressor.

Ewel (1971a), describing the pattern of ecosystem response to an intermittent stressor (Fig. 7), showed that, if the stress condition is repeated before full recovery, the system gradually loses its capacity to recover and slowly degenerates into a low-biomass steady state. This same pattern of response has been reported in salt marshes receiving chronic exposure to oil pollution (Baker, 1971) and in floodplains exposed to chronic flooding (Gardner et al., 1972).

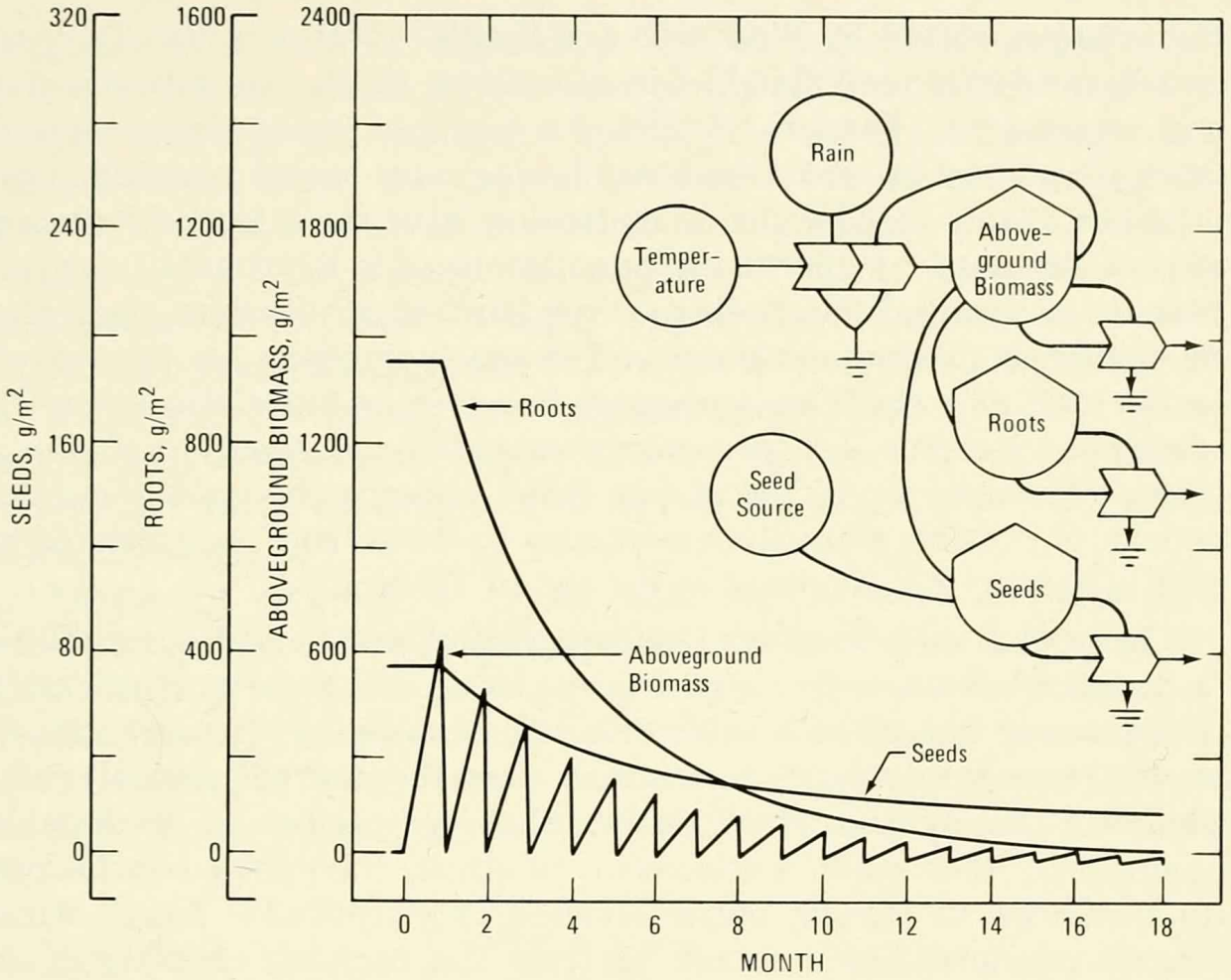

Fig. 7 Model and simulation of the effects of a chronic stressor (continuous cutting at 1-year intervals) on tropical terrestrial ecosystems [data from Ewel (1971a)]. (For identification of symbols, see Fig. 2.) Cutting is a type 4 stress (see Fig. 5). As structure is continuously removed, the system develops a steady state at a lower amount of biomass.

Stressors can also weaken systems and make them more susceptible to further stress. Woodwell and Brower (1967), for example, reported aphid population explosions induced by gamma radiation stress. The same phenomenon occurs in mangroves stressed by high salinity, frost, or alterations in drainage patterns (Lugo and Patterson Zucca, 1977). Involved in these responses are additive and/or synergistic effects among stressors which accelerate energy losses and rapidly reduce the system's capacity to negotiate more stress.

STRESS AND ECOSYSTEM COMPLEXITY

Ecologists use a variety of indexes to measure ecosystem response to stressors. Much attention has been placed on finding relationships between environmental change and species diversity or the stability of the system. [Consult the work of Baker (1970) and

the volumes edited by Woodwell and Smith (1969) and Van Dobben and Lowe-McConnell (1975) for summaries of the various theories and arguments.] Sanders (1969), for example, listed the characteristics of physically controlled and biologically accommodated communities (Table 1). The idea that stressors have the effect of reducing species diversity by increasing adaptation costs is probably correct, because a stressor, by imposing energy barriers on a system, decreases its ability to support complexity. Too much emphasis has been given to the role of a stable environment, however, without also acknowledging the balance between energy subsidies and energy drains in a given environment. All the energy flows entering the system and the variety of possible ecosystem responses to stress have been ignored in such efforts as that depicted at the top of Table 1.

Slobodkin and Sanders (1969) suggested that short-term stability (a duration of about five generations) in an otherwise unpredictable environment decreased species diversity because opportunist species would temporarily gain dominance over the normal animal component of the system. If we assume that by "periods of predictable conditions" they mean a relaxation of stress, then their conclusions do not hold in theory or in practice. Theoretically, lower stress (higher predictability?) should increase the carrying capacity of an environment. Observations in rocky tidal shores (Connell, 1972; Dayton, 1971) showed that removal of dominants by a stressor results in a temporary increase in diversity. This also occurs in high-salinity environments after a storm decreases salinity stress. At these times species diversity increases for a short period but then returns to its lower value as stressful conditions return to high intensity. Thus a property of chronically stressed ecosystems is that, during their successional patterns, species diversity may decrease rather than increase (bottom of Table 1).

Conflicting arguments about the causes of ecosystem complexity can be clarified if analyses are based on the total energy flow through the system. The productivity hypothesis of Connell and Orias (1964) was criticized by Sanders (1969), who argued that highly productive systems, such as marshes, are not necessarily diverse, as inferred from the productivity theory of ecosystem diversity. Others have argued that diverse systems are not necessarily stable (e.g., May, 1975). The argument can be restated by substituting whole ecosystem analysis for generalizations based on population studies and total energy flow per unit area (the energy signature concept) for criteria of organic productivity.

Ecosystem complexity is a function of the net energy available to a system. Net energy is the balance between the energy expenditures

associated with normal respiration and all incoming energies that contribute to ecosystem growth and complexity minus all incoming energies that tax the energy budget of the system. Slobodkin and Sanders (1969) asked the question, Why don't more species adapt to stress? The answer must be related to the high energy cost of certain adaptations vs. the energy limitations to which ecosystems and populations are exposed. In highly stressed environments we would expect strong selective pressure for the most energy-efficient solution to the stress problem; this adaptation would then win over less-efficient competitors. High efficiency, however, is not conducive to the fast rates of energy flow which are associated with lower efficiency systems.

Figure 8 presents a model that summarizes the proposed interactions and assumptions involved in maintaining ecosystem complexity. The first assumption is that the development and maintenance of ecosystem complexity involves energy expenditure. H. T. Odum (1970) proposed a formula to illustrate the rapid rise in the cost of ecosystem organization with increasing species diversity:

$$\frac{N^2 - N}{2} = \frac{fEaA}{K}$$

where N = number of species
f = fraction of the energy budget allocated to organization
Ea = energy input per unit area
A = total area of the system
K = daily cost of maintaining species interactions

The terms on the left side of the equation represent the number of possible interactions between species if organization is complete, and the terms on the right represent the amount of energy available for organization. Since the input of energy to a system is limited on a unit-area basis, the strategy of energy-resource allocation and the amount of work derived from energy transformations become significant factors in determining the competitive survival of a system.

H. T. Odum (1970) stated that, when a system has a low number of species, only a small amount of energy is allocated to organization and a larger fraction of its energy resource goes to other work functions; thus more energy is needed to eliminate a species and more energy is available to compensate for stress. Hickman (1975), for example, showed that energy allocation for reproduction increased with stress in *Polygonum* plants; he reported that as much as 71% of the energy stores goes into this function.

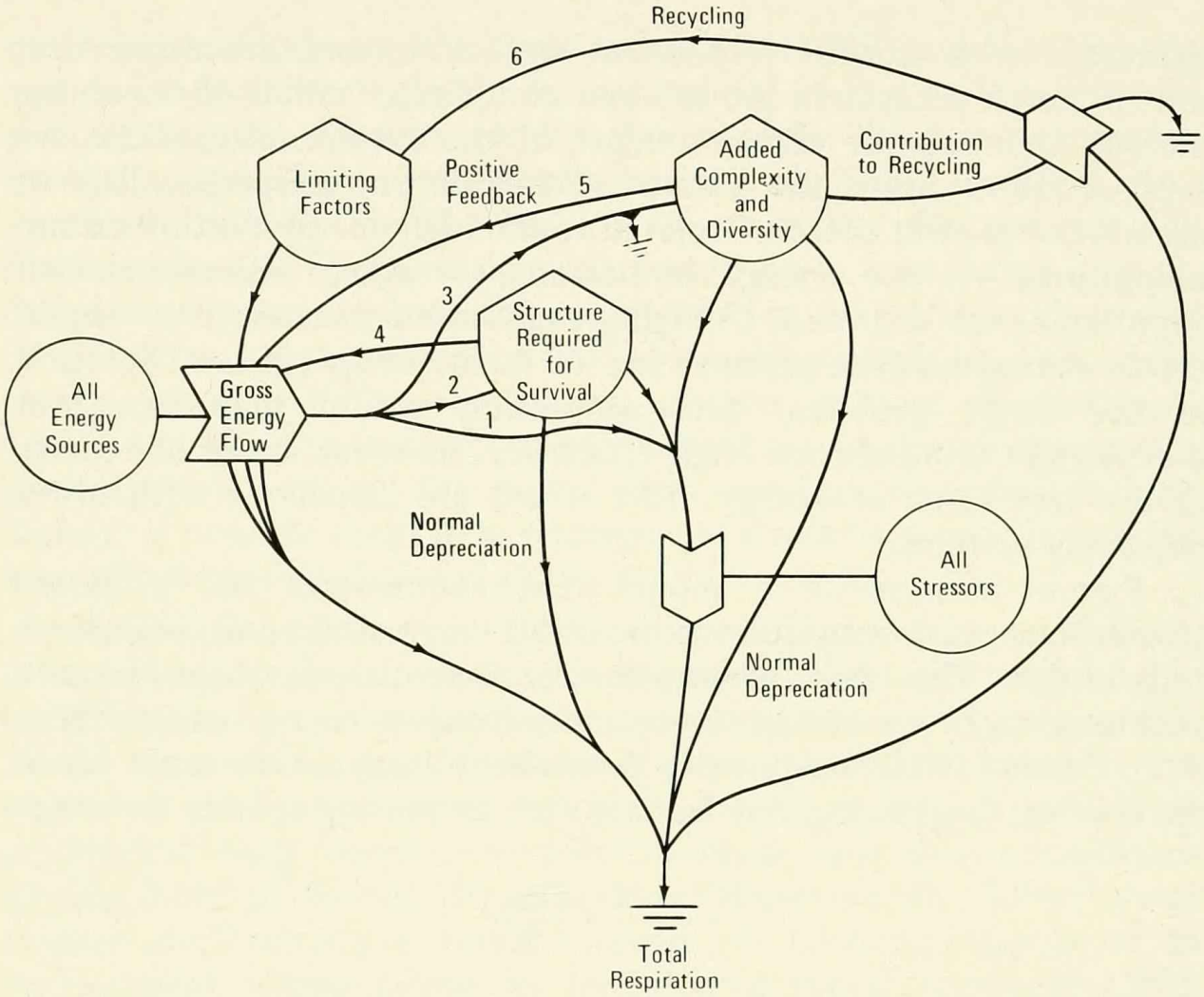

Fig. 8 Model illustrating energy flows associated with the development and maintenance of structural complexity in ecosystems. (For identification of symbols, see Fig. 2, and, for a discussion of the figure, see the text.) The gross energy flow of the system (i.e., all incoming energies that contribute to order) can be allocated to overcome disordering energies (flow 1), to develop the initial amount of structure required for survival (flow 2) and/or to develop additional complexity and species diversity (flow 3). Each of the state variables feeds back positive work that increases the ability of the system to process more energy and to use resources more efficiently. Energy allocation for structural development and complexity increases if there is net energy and if the energy investment in the feedbacks (flows 4 to 6) are offset by the increase in the energy capture and conversion efficiency of the system. As the net energy of the gross energy conversion increases (flows 1 to 3 minus flows 4 to 6), the capacity to develop more complexity and diversity also increases. Ultimately the balance between all energy sources and all stressors will determine ecosystem complexity.

A second assumption is that ecosystem complexity pays off by allowing higher efficiency in the use of energy resources and in the recycling of matter. This widely held working principle of ecology has been discussed many times (e.g., E. P. Odum, 1969; Margalef, 1969; 1975) and still makes sense to me.

The third assumption is the existence of some kind of priority development of structure in an ecosystem. Initially a minimal amount of structure necessary for survival develops. Later in successional time, if there is more net energy, complexity and diversity develop if the cost of development and maintenance do not exceed the gains that result from their feedback work. Ewel (1971b) provided evidence for the sequential development of biomass compartments in the succession of tropical ecosystems. He found that leaf biomass was the first compartment to reach steady-state values, then stems, and finally roots. The result of sequential development of compartments is a steady increase in the system's ability to use all the resources available in its surroundings. Another implication of this model is that ecosystems appear to reach functional and structural steady states early in succession, and later, with considerable lag, floristic complexity reaches its steady-state value.

In discussing ecosystem stability, we must realize that complex systems can survive only in locations with high environmental energy subsidies and low intensities of stress. An environmental change that reduces total energy flow results in a rapid decrease in structural complexity, particularly if the system loses its main power source. A decrease in complexity is interpreted as ecosystem instability. Complex cities that lose monetary subsidies, coral reefs that lose solar input energies, or complex forests growing on leached soils that lose their nutrients rapidly, lose their complexity, as expected from the behavior of the model in Fig. 8. Systems with high organic productivity but low species diversity and complexity usually export their production to other systems and, in so doing, lose the capacity to diversify. This is certainly true for mangrove forests, marshes, freshwater wetlands, some lakes, rivers, and systems stressed with high organic-matter loads. All these systems either store organics without using their potential energy or constantly export organics and receive inorganic nutrients to subsidize their primary productivity. The apparent stability of these systems is caused by the uninterrupted input of certain energy sources that represent a significant fraction of their total energy signature. Figure 6 shows evidence for this idea in relation to the role of tidal energy in maintaining stability in marshes. As long as tidal circulation continues, the marsh is capable of resisting other types of stress and recovers quickly after being subjected to a harvest or to other acute stressors. Stability is a function of stable energy input, and in most systems stability disappears when the main energy source is diverted (e.g., stress of type 1 in Fig. 5).

We have discussed how each life zone has a different background of stress which determines the potential for structural development in that locality. As more stressors are added to the background, the capacity to recover and to achieve maximum developmental potential decreases. In lowland tropical life zones, high temperatures prevail and accelerate physiological processes. For aquatic ecosystems this has serious implications for their capacity to absorb additional stress. Johannes and Betzer (1975) elaborated this point with respect to tropical marine ecosystems. Small temperature increases are very damaging to these systems; e.g., 37°C is lethal to *Thallasia* beds (Schroeder, 1975) and mangrove seedlings (Banus and Kolehmainen, 1976). These researchers also pointed out that in the tropics a higher ambient temperature and higher ambient salinity mean that a given concentration of pollutant causes a faster and greater decrease in dissolved oxygen concentration than in higher latitudes. At comparable dilution and dispersion rates, however, the pollutant concentration decreases more quickly with time and distance from the source. Thus the margin of error is smaller in tropical waters. The margin of error is equally small in ecosystems that are naturally stressed to a point near their limit of tolerance. Mangroves tolerate a more severe frost stress if they grow in low-salinity environments; they may not survive low temperatures at high soil salinities. In this case the lower salinity subsidizes high energy drains caused by frost (Lugo and Patterson Zucca, 1977).

MEASUREMENT OF STRESS AND STRESSORS AND RESEARCH NEEDS

The broad regional impact of man on the biosphere is probably why there is so much interest in studies of ecosystems and stress. Much of the research appears to ignore this broad issue, however, and instead focuses much effort on specific details that provide elegant results but do not really help society to solve the problem of coupling man to natural systems. We must document ecosystem responses to known intensities of stressors and test the ideas presented here. The researcher must take into consideration not only the intensity of the stress and the stressor but also their energy-quality characteristics relative to other energy sources impinging on the ecosystem. The points of attack in the system also require attention, and particular care should be given to the presence of feedback mechanisms and possible push—pull effects at the ecosystem level.

Table 5 summarizes some attempts at quantifying a number of stresses in natural systems and some important threshold values for specific stressors. Data of this kind, although important, are very meager. Biologists are good at counting dead or sick organisms, but little effort is made to calculate impacts per unit area or to correlate mortality with given intensities of stressors under natural conditions. Some calculations in Table 5 are based on the amount of energy actually drained from the system, but others also consider the energy the system loses when one of its components is not functioning. These unrealized energy flows are usually higher than the actual energy lost after the stressor's action. In few studies were measurements of stressor intensity and ecosystem response made (all in the same comparable units). Until researchers make these measurements, I cannot see how they will be in a position to develop a predictive capacity. For example, What is the maximum amount of energy that can be drained from an ecosystem without damaging its ability to recover? If we can learn to categorize stressors by the quality and intensity of their energy and by their point of attack in a given ecosystem and to categorize ecosystems by their energy signatures and their capacity to bounce back, then I believe we can begin to answer some of the questions about management and pollution that are being asked by those who manage natural ecosystems.

ACKNOWLEDGMENTS

I am grateful to the following colleagues for their contributions, through informal discussions, to the development of this manuscript: H. T. Odum, J. J. Ewel, S. L. Brown, C. S. Rogers, F. F. Benedict, C. A. S. Hall, S. C. Snedaker, and R. R. Twilley. None of them, however, agrees with most of this manuscript. Alma L. Lugo did most of the art work.

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TABLE 5

EXAMPLES OF CALCULATIONS OF INTENSITIES OF STRESS AND STRESSORS AND/OR OF THRESHOLDS OF ECOSYSTEM RESPONSE TO SPECIFIC STRESSORS*

Ecosystem or populations	Stressor	Intensity	Effects	Threshold	Reference
Vietnam as a whole	War	10.7% of total energy flow			Brown, 1977
Mangroves	War	40.4% of total energy flow	Extensive kills and defoliation		Brown, 1977
Estuaries	War	5.7% of total energy flow			Brown, 1977
Forests	War	7.8% of total energy flow			Brown, 1977
Agriculture	War	50% of total energy flow			Brown, 1977
Human settlements	War	12.1% of total energy flow			Brown, 1977
Eutrophic lakes	Waves		80% of end season biomass lost in submerged plants		Jupp and Spence, 1977
Mohave Desert	Rainfall			>25 mm to trigger phenology	Beatley, 1974
Volcanic slopes	Volcanic ash	1.8 m deep		<1.8 m for survival of trees; 50 cm increases growth	Eggler, 1967
Crabs *(Uca)* in salt marshes	Oil	>1000 ppm 100—200 ppm	Toxic to adults Toxic to juveniles		Krebs and Burns, 1977
Coral reefs	Waves and tides	50,000 hp	Normal wear and tear on windward zones		Munk and Sargent, 1948
	Sediments			Acute dose of 200—1000 mg/cm^2 or chronic dose of 10—20 mg/liter for mortality	Rogers, 1977

Coral reefs (cont.)	Shading	5 weeks	Significantly altered structure and function of reef	Transparency <4 m for mortality of species	Rogers, 1977
Tropical wet forest	Leaf-cutter ants' harvest	0.34 Kcal m^{-2} day^{-1}	Loss of 0.01 m^2 of leaf area/m^2, equivalent to a loss of 1.41 Kcal m^{-2} day^{-1} of productivity		Lugo et al., 1973
Granite outcrop ecosystems	Drought	Normal rainfall pattern coupled to low water storage in soil reduced growing season to about 100 days	Normal loss of unrealized productivity of about 20,000 Kcal m^{-2} growing $season^{-1}$		Lugo and J. F. McCormick, unpublished
		Additional drought caused mortality, calculated for period of 1968—1971	Plants: 506—2530 Kcal m^{-2} growing $season^{-1}$. Seeds: 66 Kcal m^{-2} growing $season^{-1}$		
Mangrove forests	Frost	−2.5 to −5.5°C	1000 Kcal m^{-2} loss as leaf biomass; 2570 Kcal m^{-2} loss as unrealized productivity		Lugo and Patterson Zucca, 1977
	Salinity			100‰; limits for growth	Cintrón et al., 1978
Oak—pine forest	Radiation			600—700 R/day increases decomposition rate	Woodwell and Marples, 1968
Lime trees	Aphids	6/leaf	Consume 19% of net primary productivity		Llewellyn, 1975
		19/tree	Consume all net primary productivity (39.74 kg/year)		

*The table is not exhaustive but shows the variety of units and methods used to report results.

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